ADAPTATIONS OF ANIMALS TO CLIMATIC EXTREMES: A REVIEW

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These three papers are important additions to the literature on body insulation, basal metabolism, heat regulation, and cold adaptation of arctic and tropical mammals and birds.

The biological literature has long been crowded with qualitative discussions of the role of fur, feathers, and fat in heat conservation. However, very few measurements have been made. Here, at last (in the first paper), Scholander, *et al.* report on the thickness of fur and fat on the mammals they studied; they actually made measurements from which the thermal conductivities could be found. The arctic work was done on winter furs of mammals at Point Barrow, Alaska. The studies were rounded out by working with tropical animals in Panamá.

Pieces of fur, taken from more thickly furred areas, were stretched tight against both sides of a round, flat hot-plate and its surrounding guard ring. The plate and ring were kept at 37° C. The fur was roughed up to give maximum insulating effect. The surrounding box, with its still air, was kept at 0°; additionally, for the beaver, polar bear and seal, there was immersion of the hide in ice water. The inner side of the skin was moistened; but as the authors point out, the temperature drop measured through the skin seems high, and is no doubt due to poor contact between skin and hot-plate. This writer would suggest that perfect contact as well as moistening might be attained by coating the skin's inner side with rather viscous Methocel solution. Methocel, a Dow Chemical Company product, is virtually inert; it can be mixed with water to almost any degree of viscosity desired.

When thus measured flatwise, it was found that the quality of the prime arctic furs and the better tropical furs was roughly constant. That is, for parallel heat flow out through a flat-stretched piece of fur, for a given temperature drop through the fur, the rate of heat flow per unit of area was inversely proportional to the fur thickness: double the thickness, and the rate of flow is halved. The charts showing what the authors call "insulation," plotted against fur thickness and against animal weight, give values as measured by the above flat method, for skin plus fur (or blubber plus skin for the seal); and is given in terms of $1/$(Cals. m²/24 hrs./1° C.). This will take on meaning if restated: it is the degrees C. drop through the skin and fur, for a rate of heat flow of one kg.-calorie per day, for an area of one square meter.

This matter of "insulation" value and its meaning is of critical importance. Several meanings of "insulation" are possible, if factors are taken only one at a time. To make this clear, consider two animals, precisely similar in every way, having a size ratio (e.g., height ratio) of 1:2. The fur thicknesses are 1:2; the surface areas are 1:4; the fur volumes are 1:8. If clipped and weighed, the two batches of fur would have a weight ratio of 1:8. Thus, if we were in business, selling such insulation, the insulation values would be 1:8; but this is a useless heat conservation criterion for the animals themselves. Starting over again, we note that the sur-

face area ratio is 1:4, and we might conclude that the insulation values are the inverse of this, or 4:1; but again, this factor alone will not tell us about the relative heat losses of the two animals. Trying another factor alone, we point to the fur thickness, and its ratio of 1:2, and might conclude that the larger animal is twice as well insulated as the smaller. This conclusion is also untenable: the factor of fur thickness alone is not sufficient. However, this last seems to be the viewpoint presented and used in the first paper. Such a concept of "insulation" may obscure some important issues. A different analysis will now be given.

Both the area and the fur thickness should be taken into account. For the above similar animals, the fur thicknesses are 1:2, tending to reduce the larger animal's loss; but the surface areas are 1:4, tending still more to increase it. Combining the two factors, we find that for the same temperature drop, the heat loss rates would be 1:2. The larger would dissipate twice as much as the smaller.

But, if the smaller animal is taken to be adequately insulated, the larger would turn out to be over-insulated. Their weight ratio is 1:8. Using the correlation of basal metabolic rate, calories per day versus weight, as adopted by Benedict or as given in the third paper, the larger animal's basal heat production rate is about five times that of the smaller. The heat production ratio is 1:5. Thus, if the larger animal were given twice the smaller one's fur thickness as assumed so far, it could dissipate at only twice the smaller one's rate through the coat, but would have five times as much heat to get rid of. Therefore, it should have considerably *less* than twice as much fur thickness.

In fact, it can be argued that the larger animal's fur thickness should be less than that of the smaller! If we adopt the *same* thickness for both, the larger has five times the heat to lose, but only four times the area to lose it from. Therefore, if the smaller animal is adequately insulated, the fur of the larger is more than adequate at the same thickness. However, the writer can see at least three considerations stepping in to prevent the adoption of less and less fur thickness as size becomes greater and greater.

First, the larger land mammals must survive while abroad or resting, under extreme exposures. The taller they are, the greater are the wind velocities at their body levels. This is a factor of real importance, but the biological literature has neglected it. Standing in the "same" wind, a moose is exposed to much higher velocities than is the marten or weasel.

Second, when an animal is lying down on cold snow—with fur compressed and the insulating value of the fur reduced—the pressure per unit of area on the fur doubles when the size is doubled. The compressing effect for a lemming-size animal is very low indeed; for a caribou it is vastly greater. Highly compressed fur is a poor insulator, due both to its reduced thickness and to its being compacted.

Third, animals are not flat, like signboards, with flat slabs of insulation stretched on them. They are made up of roughly cylindrical parts. Heat flow out through the fur is more or less divergent, or radial, in character. A 10 mm. thickness of fur on a very small animal has far from the same heat-conserving value, per unit of surface area, as the same thickness of fur on a large animal. The fact that the geometry of the case plays a major part in considering small versus large has not been adequately recognized in this kind of literature.

Turning to the animals, compare the lemming and the Eskimo dog, the weight ratio being about 1:1000, the size ratio therefore about 1:10. The lemming fur thickness is about 20 mm. If fur thickness had to obey the law of similarity, the dog would have an unwieldy 200 mm. of fur thickness. Or if we use only the factors of relative heat production and relative area, the dog should have less than 20 mm. But with the three considerations in mind, it is not surprising to find that the dog actually has about 40 mm., or about twice that of the lemming. Moreover, the dog can sleep outdoors through the arctic weather, and the lemming cannot. Also with the foregoing arguments in mind, we are not surprised to learn from the paper that when the size of the fox or dog is reached, increase of size occasions little change in fur thickness.

"From the size of a fox to the size of a moose there is no correlation between insulation and

body size, they all have about the same insulation per surface area" is one of the conclusions. This must first be corrected to read, per *unit* of surface area. They then do have "about the same insulation," when measured flatwise as described in the paper. But when the geometry of flow (the radial flow effect) in the fur, as actually worn, is taken into account, the insulating effect for the smaller of these animals is less than it at first seems to be.

The data secured are valuable. Eventually, when geometry of heat flow, habits of the animals in evading or accepting extreme exposure, wind effect related to size, and compression of fur when resting or sleeping—when these various considerations can be evaluated and weighted into the analysis, we may eventually be able to work out a very good correlation of fur-thickness with size.

An attempt was made to secure insulation measurements for snow bunting and ptarmigan skins. "However, these measurements are less satisfactory since it is impossible to produce on the test plate the well-ordered elevation of the feathers which the live bird can achieve to produce maximum insulation." That is, flatwise testing of small skins does not work out well. This points to the need for developing test methods in which skins will have more nearly their natural conformation, by stretching them over cylinders or spheres, or even models of the animals themselves.

The paper has some good discussion of animal heat loss as affected by vasomotor control, and of the way the legs and feet of arctic animals are adapted to tolerate extreme cold exposure and at the same time reduce heat loss, by permitting these members to go to low temperatures.

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The second paper gives valuable new data on basal metabolic rates and heat regulation for arctic and tropical mammals and birds. The mammals studied at Point Barrow were the white fox, Eskimo dog, polar bear (cub), ground squirrel, lemming and weasel; the birds, the Glaucous Gull (*Larus hyperboreus*), Canada Jay (*Perisoreus canadensis*) and Snow Bunting (*Plectrophenax nivalis*). The Panamá mammals were the two-toed sloth, night monkey, marmoset, raccoon, coati and jungle rat; the birds, the Yellow-thighed Manakin (*Pipra mentalis*) and Pauraque (*Nyctidromus albicollis*).

Measurements of metabolic rates were made in a controlled-temperature respiration chamber, the heat production being determined by the oxygen consumption or carbon dioxide production. Each animal was started in its thermoneutral zone. Within this zone of lowest metabolic rate (conditions being that the animal is awake, resting, and in the post-absorptive state) lowering the chamber air temperature does not change the rate of heat production or heat loss. Instead, the animal compensates for the increased cold exposure by pilomotor erection of fur or feathers, which increases the insulating value of the coat; by vasomotor control of heat carried by the blood to skin and limbs; by vasomotor control of temperature of these parts; by changes in posture, and so on. At the lower end of the zone the critical temperature is reached. As the chamber temperature is lowered below the critical, step by step, heat loss is more and more increased; and the body maintains its temperature by resort to shivering, so that muscle energy turned into heat causes heat production to keep even with heat loss. This is observed in terms of the rising metabolic rate.

The authors described a conceptual mechanical model, housed in a controlled-temperature chamber, which would have a heat source, thermostatic control, and insulation variable automatically up to a maximum. Up to this limit the model would perform within its thermoneutral zone; heat production and heat loss would be held constant by variation of the insulation. Thereafter, as the test chamber is cooled further, heat loss would rise, and the thermostat would operate to make the heat production rise with the loss. The animals are then interpreted in terms of such a model.

The model would have only simple insulation in the true or technical sense; whereas, for the animals insulation "means the sum total of all factors, such as fur, skin and tissue cool-

ing, and posture, that impede the loss of heat from the animal" (p. 249). The reader of this paper may seriously misinterpret its findings unless he carefully takes note of this broadened use of the term *insulation*. Also, it is regrettable that this term, which is needed for what it heretofore has meant, should be so broadly construed. Some other term or phrase, such as *heat conserving ability*, should have been used to denote the over-all effect of the several factors.

The tropical animals display much greater temperature sensitivity than the arctic animals. As the test chamber temperature is progressively lowered, they reach their critical temperatures much sooner, and their metabolic rates thereafter rise much faster than those of the arctic animals. The difference is not accounted for solely by difference in thickness or quality of the fur or feathers. As is brought out, much of the difference in sensitivity comes from differences in adaptive heat regulation factors displayed by the extended parts of the body— the face, limbs and feet. The tropical animal has not had to meet extended cold threats; and when so exposed, the extended parts tend to maintain their temperatures. The arctic animal has had to adapt in order to live through what we tend to consider intense cold exposure; and a major factor of adaptation is its ability to let limbs and feet get along with little heat supplied from the central body mass, accompanied by the fact that normal (and presumably perfectly comfortable) tissue temperatures in the extended parts may be down near 0°. This was demonstrated for the aquatics, and presumably holds for the terrestrials.

Nothing about research is more typical than its tendency to indicate still more research. Plenty of interesting work remains to be done to round out the picture and lend verification. Using thermocouples, the same arctic and tropical species should be studied, to measure skin temperatures and even internal temperatures at various depths, for the extended parts and for the trunk as well. In fact, a little of this work was done at Point Barrow.

It is very interesting to note that Point Barrow failed to furnish weather cold enough to cool the test chamber down to the critical temperature for the foxes and dogs. Two foxes were flown to the Naval Research Laboratory in Washington, D.C., where shivering was induced by −70° chamber temperature.

In discussing the ability of arctic mammals to stand cold extremes, the authors would have done well to mention the fact that the insulating quality of entrapped air materially improves with the low temperatures encountered by these animals. Taking the thermal conductivity of air at 40° as a base, the conductivity at −40° is about 80% as great; and at −70°, about 70%. This must be of real importance in arctic survival.

The third paper opens by contrasting the extremes of the thermal environment of Point Barrow with the relatively constant environment at Barro Colorado. Body temperature and climatic adaptation are then discussed, and it is shown that with few exceptions—all moderate in degree—mammals and birds the world over have body temperatures falling within a narrow temperature band. That is, the homoiothermic animal, broadly speaking, does not adapt to climate by change of body temperature. Insulation and climatic adaptation are taken up next; and here, of course, it is brought out that change in amount of insulation is a major adaptive factor. Also, if we follow the authors when they include, under the term insulation, vasomotor regulation permitting body extremities to drop in temperature, then it can be said that: "The cold legs of arctic aquatic birds and mammals (and probably of the terrestrial forms as well) may be taken as another example of adaptive insulation" (p. 262).

The paper presents new data on basal metabolic rates, showing them in relation to the standard mouse-to-elephant curve of kg.-calories per day plotted against weight. All of the arctic and tropical mammals fall on or close to the curve, except that the weasel is quite high (two or three times the expected value) and the sloths, with their labile temperatures, are low. The authors apparently accept the arctic weasel as an exception and they point, in this connection, to what they believe to be an insulating coat thin enough to go along with the apparently higher basal rate. "Hence we are forced to conclude that our arctic weasels had a greatly increased

resting metabolic rate compared with the southern form. This may possibly mean a metabolic adjustment to cold" (p. 265). The exception is so striking—as is the conclusion forced upon us if it is proved—that further research on the northern form surely is in order.

The weasel is an extremely active animal. Benedict was meticulously careful to make sure his animals were in a truly resting state before he accepted a metabolic rate as basal. He also found that unless a wild animal became accustomed to test conditions, rates were high even at rest. The weasel is prone to be defiant and restless. In further tests, steps should be taken to make sure that both criteria are met. It may even be necessary to duplicate, on the weasel, Hoover's work on the rat, by killing the animal, quickly measuring metabolic rates for the several main types of tissue, allowing for heart and respiratory activity, and summing up.

New data on birds are also presented. Much less is known about basal rates for birds than for mammals. However, "Two of our night hawks [Pauraques] are very low, and this is probably due to their faculty for hibernation" (p. 265). The two Glaucous Gulls studied were high. But, as is said: "More material is necessary before we can tell whether the basal metabolism in birds may be adaptive to climate" (*loc. cit.*).

The critical temperature, to repeat, is the lower limit of the thermoneutral zone. The difference between this and the body temperature is called "critical temperature gradient" by the authors. For four arctic and seven tropical species, they give the value as observed; and also, as calculated by use of basal rate, body insulation as measured, and surface area as computed by the Meeh formula. In spite of the over-simplification inherent in the calculating method, the agreement between observed and predicted values is surprisingly good in most cases.

The critical temperature *gradient* just mentioned should have been called the critical temperature *difference*. The general excellence of these three papers may tend to induce some workers to adopt all of their usages. However, very strong objection must be entered against the misuse of the term *gradient* which, throughout the papers, is almost always used when *temperature difference* is what is intended.

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